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SELECTION WITHIN AND ACROSS POPULATIONS IN LIVESTOCK IMPROVEMENT[1]

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ABSTRACT

Genetic evaluations within and across populations (countries, breeds, herds) allow ranking on estimated genetic merit and selecting breeding individuals across populations. Selection within and across populations (combined selection) should by definition always be as good as, or better than, within-population selection, the limiting case. The advantage depends on the sizes of the populations, the number of populations, the initial genetic means, and the correspondence of the breeding objectives in the different populations, as measured by the genetic correlation for economic merit. The advantages of combined selection are evaluated deterministically for a simple case of selecting the best males for use across populations by using a common truncation line over the distributions of EBV for the different populations. Combined selection increases overall response rates in the cooperating populations. Where the initial genetic means are the same, small populations (100 males tested) benefit greatly from combined selection. Large populations (500 to 1,000 males tested) also benefit, but less. The results depend on the increased selection response to scale, response being approximately linear with the logarithm of the number tested. When the initial means differ, the genetically poorer population can catch up in three to five generations and then contribute to the increased responses with combined selection. When breeding objectives differ, selection usually gradually pulls the populations apart and they make less and less contribution to each other and finally become separate. These results have implications for breeding strategies. Their application would affect structures of populations and rates of genetic change possible by selection.
Key Words: Selection, Genetic Gain, Livestock, Populations

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Introduction

There is great variety of breeding improvement systems in livestock breeding and in their respective achievements (Smith, 1984). At the one extreme, poultry are bred by a small number of international breeding companies, each with a limited number (5 to 15) of breeding lines of limited size (5,000 to 20,000 tested) at one or a few locations. At the other extreme, in cattle breeding most countries have a large number of breeding herds with small numbers (50 to 200) per herd and large-scale field testing and evaluation systems. Sheep systems follow those of cattle, and both systems are found in pig breeding. The species with concentrated breeding units have achieved more relative to that deemed possible (Smith, 1984) than those with larger, dispersed breeding populations and larger investments.

The estimation of genetic differences of populations and the availability of EBV for dairy sires across countries (Banos et al., 1991) prompted study of methods of selecting bull sires across countries (here called combined selection) and evaluation of the benefits (Banos and Smith, 1991). A similar approach has been used here to study the value of combined selection in any species for populations of different sizes, different breeding goals, and different genetic means over a number of generations. The populations could refer to countries, stocks (breeds or strains), or

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to herds within breeds. The objective is to provide an overview of the benefits of combined selection to selection response. The genetic evaluations across populations would be possible through exchange of breeding material, either by using field data from breeder import-export exchange, or in an organized (experimental) manner (King et al., 1975; Stolzman et al., 1981).

Methods

Consider the simple case of selection *within* a population with N males and N females tested, representing the size of the population. The populations considered are the breeding populations in which the genetic improvement is made. The commercial stocks will be bred from the breeding populations and will lag genetically behind them. Selection in the breeding population is on EBV for economic merit, ignoring information on relatives, and simply estimated from the genetic mean of the population and the genetic deviation from the mean, measured as h^2P, where P is the phenotypic deviation and h^2 is the heritability. The standard deviation of the EBV is $h^2\sigma$, where σ is the phenotypic standard deviation of economic merit. Let the subscripts m and f denote male and female, respectively. To limit inbreeding a fixed number (M) of males is selected and used, the proportion being p_m = M/N and intensity of selection i_m. With limited female reproductive rate, a fixed proportion p_f of females is selected with intensity i_f. The genetic response per generation to selection is predicted as $.5(i_m + i_f)h^2\sigma$.

Consider now two populations (1 and 2) having the same breeding objective (H) and genetic means (G_1 and G_2) and with N_1 and N_2 males and N_1 and N_2 females tested, respectively. For simplicity females are selected within populations, but the best males, identified by ranking on EBV across populations, are used across populations by artificial insemination. The proportion (p_{im}) of males to select from population i is found by using a common truncation point across the EBV distributions for the two populations, such that the best M males are selected (Smith and Ruane, 1987; Ducrocq and Quaas, 1988). The new genetic mean for population 1 is

$$.5\left[\frac{N_1p_{1m}(G_1 + i_{1m}h^2\sigma) + N_2p_{2m}(G_2 + i_{2m}h^2\sigma)}{N_1p_{1m} + N_2p_{2m}} + (G_1 + i_f\ h^2\sigma)\right], \qquad [1]$$

and similarly for population 2. The term for females could be elaborated in the same way to allow for selection of females across populations. The formulation [1] allows us to deal with populations of different sizes and different genetic means and to compare within-population means and responses with those for combined selection across populations. It can also be extended to cover several populations.

The populations may have different breeding objectives, H_1 and H_2 and different means for each objective (G_{11} and G_{12} for population 1 and G_{21} and G_{22} for population 2). Let h^2_1 and h^2_2 be the heritabilities of the two objectives and let R be the genetic correlation between the objectives. With combined selection for H_1, the genetic means for H_1 and H_2 in population 1 become

$$G^*_{11} = .5\left[\frac{N_1p_{11m}(G_{11} + i_{11m}h^2_1\sigma_1) + N_2p_{21m}(G_{21} + i_{21m}h^2_1\sigma_1)}{N_1p_{11m} + N_2p_{21m}} + (G_{11} + i_{11f}\ h^2_1\sigma_1)\right],$$

and

$$G^*_{12} = .5\left[\frac{N_1p_{11m}(G_{12} + Ri_{11m}h_1h_2\sigma_2) + N_2p_{21m}(G_{22} + Ri_{21m}h_1h_2\sigma_2)}{N_1p_{11m} + N_2p_{21m}} + (G_{12} + Ri_{11f}h_1h_2\sigma_2)\right]$$

where, for example, p_{21m} is the proportion of males selected from population 2 and used for breeding in population 1, and similarly for G^*_{21} and G^*_{22}. This allows us to deterministically track the responses and means for the two objectives in the two populations over the generations.

The approach has been kept simple to study the main features and results of combined selection. Thus, it is assumed that the genetic variance has reached a selection equilibrium (Bulmer, 1971) and the heritabilities refer to this genetic situation. In a similar study on the use of international dairy sire rankings across

TABLE 1. SELECTION RESPONSES PER GENERATION WITH SELECTION ACROSS TWO POPULATIONS (COMBINED SELECTION) AND WITHIN POPULATIONS, WITH DIFFERENT NUMBERS TESTED PER POPULATION[a]

No. of males tested		Selection response per generation (SD units)				
Population		Combined	Within-population selection			
1	2	selection (C)	1	C/1[b]	2	C/2[b]
100	100	.265	.230	1.16	.230	1.16
	500	.319	.230	1.39	.314	1.02
	1,000	.346	.230	1.51	.344	1.01
500	500	.342	.314	1.09	.314	1.09
	1,000	.359	.314	1.15	.344	1.04
1,000	1,000	.371	.344	1.08	.344	1.08
	10,000	.434	.344	1.26	.433	1.00
10,000	10,000	.454	.433	1.05	.433	1.05

[a]The two populations have the same initial genetic mean and the same breeding objective. Heritability = .25, 10 males used per population, .95 of females used per population.

[b]Ratio of the response with combined selection (C) to the response from selection within population 1 (C/1) or population 2 (C/2).

countries, Banos and Smith (1991) took account of the loss of genetic variation and the depression of performance due to inbreeding and, using results of Goddard and Smith (1990), developed an algorithm to optimize the number of bull sires and maximize response for a given time horizon. However, the number of bull sires selected was fairly constant (7 to 10); a simpler approach of dealing with a fixed number of selected males has been used here. No allowance has been made either for inbreeding or for the time horizon, which are taken to be the same for selection within populations and for combined selection.

In estimating breeding values, information from all relatives could be used in BLUP to increase the accuracy of selection (expressed as the standard deviation of EBV) and thus the response rates. This would also tend to increase the rate of inbreeding due to selection of related individuals, so less intense selection could be practiced if a common rate of inbreeding were sought. The advantage of BLUP selection over selection on phenotype, with the same number tested and the same inbreeding incurred, is being re-appraised.

Results

The value of combined selection relative to selection within a population, for a simple case with the same breeding objective and the same initial genetic means, is shown in Table 1 for sets of two populations of different sizes. With combined selection, the overall genetic response is greater than for within-population selection, so both populations benefit. This is due to increasing response from increases in scale (numbers tested), the responses being approximately linear on the logarithm of the number tested (Smith, 1981). The larger number tested allows higher selection intensity in males, exploiting the high reproductive rates possible by artificial insemination. Small populations benefit most from combined selection, whereas large populations gain little from combining with small populations. Combining with populations of the same size, moderate gains (5 to 15%) in response are obtained. The extra responses were a little smaller than those shown by Banos and Smith (1991). They took account of inbreeding and optimized the response. This led to less intense selection and less response in small populations than in large populations, so the relative responses were larger.

Examples of the effects of selecting more males and selecting among females within populations are given in Table 2. As more males are selected and the selection intensity falls, the value of combined selection increases. This is especially true in small populations (e.g., relative responses of 1.16 vs 1.52 for populations of 100 tested in row 1 of Table 2), where the within-population selection intensity is low. With the same genetic means, the proportional benefit of combined selection in the simple case is the same for any heritability, as can be seen from the form of expression [1]. More intense selection of

TABLE 2. RELATIVE GENETIC RESPONSE BY SELECTION OF MALES ACROSS TWO POPULATIONS (COMBINED SELECTION) TO SELECTION RESPONSE WITHIN POPULATIONS[a]

Proportion of females selected	No. of males tested		No. of males selected			
			10		50	
	Population		Population		Population	
	1	2	1	2	1	2
.95	100	100	1.16	1.16	1.52	1.52
		500	1.39	1.02	2.16	1.04
		1,000	1.51	1.01	2.45	1.02
	500	500	1.09	1.09	1.16	1.16
		1,000	1.15	1.04	1.25	1.07
	1,000	1,000	1.08	1.08	1.13	1.13
		10,000	1.26	1.00	1.40	1.01
	10,000	10,000	1.05	1.05	1.07	1.07
.50	100	100	1.11	1.11	1.29	1.29
		500	1.29	1.01	1.66	1.03
		1,000	1.37	1.00	1.82	1.01
	500	500	1.07	1.07	1.12	1.12
		1,000	1.11	1.03	1.18	1.06
	1,000	1,000	1.06	1.06	1.09	1.09
		10,000	1.21	1.00	1.30	1.01
	10,000	10,000	1.04	1.04	1.06	1.06

[a]The two populations have the same initial genetic mean and the same breeding objective.

females, for example by increasing reproductive rates, provides more selection response due to female selection within populations and dampens the benefits of combined selection unless females are also selected across populations (see below).

The value of combining several populations of the same size is evaluated in Table 3, omitting female selection for simplicity. Again, the results are due to increases in scale, as before being approximately linear on the logarithm of the number of individuals tested, except where the selection intensity is low with one population tested. With more populations combining, increased overall responses are obtained, but at a declining rate.

It is unlikely that two populations would have the same genetic mean. The population with the higher mean will have more to contribute initially and will gain less from combined selection until the other population catches up. An example is given in Table 4. With an initial superiority of one SD, population 1 contributes most of the males in the early generations but gains little then in extra combined response, as can be seen from the high proportion of males selected from population 1. Gradually, over three to five generations, population 2 catches up and contributes its share of selected males, and the extra

TABLE 3. RATIOS OF COMBINED GENETIC RESPONSE TO WITHIN POPULATION RESPONSES WITH SEVERAL POPULATIONS COMBINING (NO FEMALE SELECTION)[a]

No. of males selected	No. of males tested per population	No. of populations			
		1	2	5	10
10	100	1.00	1.18	1.40	1.54
	500	1.00	1.10	1.22	1.31
	1,000	1.00	1.08	1.19	1.26
	10,000	1.00	1.06	1.13	1.18
50	100	1.00	1.59	2.19	2.58
	500	1.00	1.18	1.40	1.51
	1,000	1.00	1.13	1.29	1.40
	10,000	1.00	1.07	1.16	1.23

[a]The populations have the same initial genetic mean and the same breeding objective.

TABLE 4. EFFECT[a] OF A DIFFERENCE IN THE INITIAL GENETIC MEANS ON COMBINED SELECTION FOR TWO POPULATIONS[b]

	Population			
	1		2	
Generation	Genetic mean	Proportion of males selected	Genetic mean	Proportion of males selected
0	1.00	1.00	.00	.00
1	1.32	.99	.82	.01
2	1.64	.90	1.39	.10
3	1.96	.74	1.83	.26
4	2.29	.63	2.23	.37
5	2.63	.56	2.60	.44
6	2.98	.53	2.96	.47
7	3.34	.52	3.33	.48
8	3.69	.51	3.68	.49
9	4.05	.51	4.04	.49
10	4.40	.50	4.40	.50

[a]In standard deviation units.

[b]The two populations have the same breeding objective; 500 males are tested and 50 males are selected per population. Heritability = .25.

response from combined selection is then also obtained in population 1. The relative benefits of combined selection will depend on the heritability that affects the size of the within-population selection response relative to the initial difference in the means. In practice, with a large initial genetic difference, selection and use of females across populations will also be used to upgrade the poorer population more quickly and reduce the lag period. At the extreme, if one population is much superior to the other, all the males and females for breeding in both populations will come from the best population, costs and feasibility permitting. The one population will then replace the other. In the next generation the genetic means of the two populations will be the same, and combined selection will benefit both populations, as shown in Table 1.

So far selection has been for the same breeding objective in both populations. With different objectives, expressed by the genetic

TABLE 5. RELATIVE GENETIC RESPONSES[a] AND SOURCE OF SELECTED MALES IN TWO POPULATIONS WHERE THE GENETIC CORRELATION BETWEEN BREEDING OBJECTIVES IS .75[b]

	Cumulative genetic response (SD units)			
Generation	Within-population selection	Across-population selection	Ratio	Proportion of selected males from the other population
1	.23	.27	1.17	.50
2	.46	.53	1.15	.36
3	.70	.78	1.11	.28
4	.93	1.02	1.10	.23
5	1.16	1.26	1.09	.18
6	1.39	1.50	1.08	.14
7	1.63	1.74	1.07	.10
8	1.86	1.97	1.06	.07
9	2.09	2.20	1.05	.05
10	2.32	2.44	1.05	.03

[a]In standard deviation units.

[b]The two populations have the same initial genetic means for the two breeding objectives; 500 males and 500 females are tested per population, 50 males are used per population. Female selection is .95 and heritability = .25 for both objectives.

TABLE 6. RELATIVE GENETIC RESPONSE AFTER FIVE GENERATIONS OF SELECTION OF MALES ACROSS TWO POPULATIONS (COMBINED SELECTION) AND SELECTION WITHIN POPULATION FOR DIFFERENT GENETIC CORRELATIONS OF BREEDING OBJECTIVES OF THE TWO POPULATIONS[a]

No. of males selected	Proportion of females selected	No. tested		Genetic correlation									
		Population		1.0		.9		.75		.5		.25	
				Population									
		1	2	1	2	1	2	1	2	1	2	1	2
10	.5	100	100	1.11	1.11	1.08	1.08	1.05	1.05	1.03	1.03	1.02	1.02
			500	1.29	1.01	1.22	1.01	1.14	1.00	1.07	1.00	1.06	1.00
			1,000	1.37	1.00	1.29	1.00	1.19	1.00	1.10	1.00	1.08	1.00
		500	500	1.07	1.07	1.04	1.04	1.02	1.02	1.01	1.01	1.01	1.01
			1,000	1.11	1.03	1.07	1.02	1.03	1.01	1.02	1.00	1.02	1.00
		1,000	1,000	1.06	1.06	1.03	1.03	1.01	1.01	1.01	1.01	1.01	1.01
50	.5	100	100	1.29	1.29	1.26	1.26	1.20	1.20	1.13	1.13	1.09	1.09
			500	1.66	1.07	1.57	1.02	1.44	1.01	1.29	1.00	1.20	1.00
			1,000	1.82	1.01	1.72	1.01	1.57	1.00	1.37	1.00	1.25	1.00
		500	500	1.12	1.12	1.09	1.09	1.05	1.05	1.03	1.03	1.02	1.02
			1,000	1.18	1.06	1.13	1.04	1.08	1.02	1.05	1.00	1.04	1.00
		1,000	1,000	1.09	1.09	1.06	1.06	1.03	1.03	1.02	1.02	1.02	1.02

[a]The two populations have the same initial genetic means. Heritability = .25 for both objectives.

correlation in economic merit between them, combined selection is less useful and declines in value as the populations pull apart. An example is given in Table 5 for two populations with the same initial genetic mean for the two traits, the same heritabilities, and a genetic correlation of .75. Initially, combined selection is useful, but as the populations pull apart, it contributes less and the gene flow across populations decreases. The early advantage is maintained, but the ratio of combined to within-population selection response declines over time. The effect of different genetic correlations is shown in Table 6. At any particular time (here, the fifth generation) the extra response with combined selection falls as the genetic correlation declines. With high genetic correlations, an equilibrium may be reached where the proportion selected from the different populations then stays constant over the generations. Some examples are given in Table 7. In these cases it is worthwhile for the populations to continue together. This applies especially to small populations, it being better to combine with a larger population, even though the breeding goal is somewhat different. The results for different breeding objectives will depend on the initial genetic means (for both objectives in both populations) and on the heritabilities of the two objectives. These can be determined from the expression for G^*_{11} and G^*_{12} given above.

Discussion

Combined selection across populations is by definition as good as or better than within-population selection, which is the limiting case. It maximizes the expected genetic means in the next generation by finding a common truncation line across the distributions of EBV. It thus depends on having interbreeding across populations with enough genetic ties existing or created between populations so that population genetic means can be well estimated. If EBV are expressed relative to a common genetic base, then populations can be ignored and selection based simply on EBV. The advantage of combined selection comes from increased scale, having a larger total pool of tested animals to select from, yet maintaining the same number of breeding sires. This is possible by using the very high male reproductive rates with artificial insemination and the transfer of semen across populations. Poorer populations can catch up quickly and then will contribute to the benefits of combined selection. In the species of farm livestock that are large in size, such as cattle, sheep, and pigs, very large numbers of candidate breeding animals or their progeny are recorded or tested annually in the national field recording-evaluation systems. Yet, until recently with international use of North American Holsteins, little use was made of other populations, and

TABLE 7. EXAMPLES OF EQUILIBRIA IN SELECTING ACROSS TWO POPULATIONS WHEN THE GENETIC CORRELATION BETWEEN BREEDING OBJECTIVES IS LESS THAN ONE[a]

No. of males tested					
Population		Genetic correlation	Generation at equilibrium	Ratio of no. selected for 1 from 1 and 2	Ratio of combined to individual response in 1 at equilibrium
1	2				
100	500	.95	17	.31	1.23
		.90	33	.55	1.16
		.85	43	1.36	1.08
		.80	—	No equilibrium	
500	500	.98	19	1.23	1.06
		.95	42	1.96	1.04
		.90	—	No equilbirum	—

[a]The two populations have the same initial genetic means for both breeding objectives. Heritability = .25 for both objectives. Ten males are used per population and .50 of females are selected within population.

the advantages of scale of the total testing effort have not been realized. Nor have they been used to predict the rates of genetic response possible if the testing and evaluation efforts across countries were combined. In poultry breeding, in the hands of a small number of international breeding companies, the scale of testing (5,000 to 20,000 tested per population) is limited by cost, and combined selection is not possible because of their competitive position.

There are some benefits from keeping populations separate, even if their breeding objectives are the same. Having two or more populations allows flexibility in use and acts as insurance against loss (for example by disease) or chance effects such as genetic anomaly or genetic drift. Duplication may provide competition between populations to make more progress and increase market share. Another advantage could come from crossing populations to benefit from heterosis in commercial production using crossbreds. Heterosis, on the other hand, may cause difficulties in evaluating the additive genetic merit of population crosses, and in evaluating sires if their progeny differ in levels of heterosis expected (Van der Werf, 1990). There is a risk due to genetic drift that may affect actual response obtained. The risk can be gauged from the variance in expected response (Hill, 1980; Goddard and Smith, 1990). It may be appreciable in the short term with a small number (< 10) of sires used per generation, but it becomes less important with more sires and over generations as total response accumulates.

The genetic correlation as applied to breeding objectives implies that individuals can be ranked for both objectives over both populations. Genotype × environment interactions may also cause the genetic correlations between objectives to be less than unity. Parents can be tested (through their progeny) in several environments, but individuals can only be tested phenotypically in one environment, and thus can only be evaluated and ranked in that environment. Thus, the methods used here do not apply to the genotype × environment interaction. However, genotype × environment interactions across countries with temperate climates and good husbandry conditions have not been found to be important or consistent (e.g., Carabano et al., 1990). However, it is clear from the results here that interactions leading to genetic correlations less than .8 to .9 would be large enough to remove the benefits of combined selection.

Implications

Combined selection can increase overall response rates, so cooperation among breeding populations (countries, breeds, herds) is worthwhile. Populations with low genetic levels and small populations, or populations testing small numbers of males, are likely to benefit most from combining with other populations. Thus, with estimation of breeding values across populations, open breeding systems can exploit initial differences, benefit from combined selection, and maximize overall response rates. Breeds and breeders should exploit these

advantages to improve their competitive position and enhance their genetic gains.

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